

Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

VOL. 125, No. 2

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ON THE MAJOR ARTERIAL CANALS  
IN THE EAR-REGION OF TESTUDINOID TURTLES  
AND THE CLASSIFICATION OF THE  
TESTUDINOIDEA

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CAMBRIDGE, MASS., U.S.A.

PRINTED FOR THE MUSEUM

JUNE, 1961



No. 2 — *On the major arterial canals in the ear-region of Testudinoid Turtles and the classification of the Testudinoidea*

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That there is an osteological difference in cranial foramina between typical emydine and testudinine turtles, on the one hand, and kinosternines (mud-turtles), on the other, has been known for some time. Siebenrock illustrated (1897, pl. 2, fig. 8) the inner view of the cranial chamber of "*Cinosternum odoratum*" (= *Sternotherus odoratus*) and showed a foramen labeled f.c.i.' = "Foramen caroticum internum, Zweig zur Augenhohle hinziehend" that does not appear in his figures of other Testudinoidea (*Chelydra serpentina*, *Testudo* (sic, = *Psammobates) tentoria*, *Cyclemys dhor* (= *C. dentata*), and *Geoemyda spinosa*). I can find no discussion in Siebenrock's text on this foramen in "*Cinosternum*."

A more striking difference, because it is more easily observed, was still earlier noted by Baur (1888b), who found that an arterial foramen between the pro-otic and quadrate seen in nearly all turtles is greatly reduced or absent in *Dermatemys*, *Staurotypus*, and the kinosternines. This feature was confirmed by Bienz (1895) and is cited, as one of many osteological characters, in the classification of turtles by Romer (1956).

But while this characteristic has long been known in terms of osteology, there is no work, to my knowledge, describing the difference between mud-turtles and pond-turtles in the arterial supply of the head. Since closure of a large arterial foramen implies considerable rearrangement of the head arteries, a knowledge of the arteries would seem essential to interpretation of the osteological features.

Dissection of *Kinosternon subrubrum* and *Sternotherus odoratus* (kinosternid foramen-pattern) and of *Malaaclemys* (*Graptemys*) *geographica*, *Chrysemys* (*Trachemys*) *scripta*, *Chrysemys picta*, *Gopherus berlandieri*, *Testudo* (*Testudo*) *graecca*, *Ocadia sinensis*, *Chinemys reevesi*, *Clemmys insculpta*, *Emys orbicularis* (Kunkel's series F slides, Kunkel, 1912), and *Chelydra serpentina* (juvenile) (testudinid foramen pattern) convinces me that the two foramen patterns are indicative of two quite different adult arterial patterns, and further, that neither arterial pattern

can be derived directly from the other one, although both may be derived from a more generalized pattern, such as that seen in living Cheloniidae.

## I. THE PATTERN OF THE TESTUDINIDAE

*Bony canals and foramina:* — There is an opening on the rear surface of the skull, called the posterior aperture by some authors = the foramen jugulare internum of Siebenrock (1897), the fenestra postotica of Nick (1913). This opening is bounded laterally by the quadrate, ventrally by the pterygoid, and medio-dorsally by a vertical lamina of the opisthotic or the exoccipital or the two bones together. (Since this lamina represents a posterior protection for the peculiar pericapsular extension of the perilymphatic sinus characteristic of turtles, I propose to call it the crista postperilymphatica, *new term.*) Nick's name for the opening, fenestra postotica, seems more fortunate than Siebenrock's name, foramen jugulare internum, since the opening rarely contains the strict homologue of the mammalian vena jugularis interna. Rather, it contains the main reptilian head-vein, the vena capitis lateralis, sometimes called, by analogy, the "internal jugular," but more nearly homologous to the mammalian sinus cavernosus. The turtle homologue of the mammalian vena jugularis interna is a rather small vein closely bound to the vagus nerve, and with the nerve piercing the crista postperilymphatica by an opening I here call the apertura vagi, *new term.*<sup>1</sup> The vein and vagus may then be followed deeper within the skull and be seen to enter the true foramen vagi or foramen jugulare between opisthotic and exoccipital. The vena jugularis interna then extends mediad in the dura mater above the brain (cf. mammalian sinus transversus) to join a longitudinal vein in the dura mater on the midline above the brain (cf. mammalian sinus sagittalis superior). In

<sup>1</sup>Throughout this paper in dealing with openings in the dried skull for cranial nerves, I have used the word "foramen" for holes in the primary braincase, and the word "apertura" for holes in the secondary investments of the primary braincase. This convention is particularly necessary in dealing with holes for transit of the glossopharyngeal nerve; in such turtles as *Orlitia* this nerve pierces bone three times: (1) an internal glossopharyngeal foramen leading from the cranial cavity into the inner ear cavity of the dried skull, (2) an external glossopharyngeal foramen from the inner ear capsule to the pericapsular space, and (3) a glossopharyngeal aperture in the crista postperilymphatica (a secondary investment of the primary braincase). The second hole is invariably present in turtles; the first is often undefined by bone in young turtles, but is probably constant for all fully mature skulls. The third hole is absent in adults of many turtles. Without a convention the name "external glossopharyngeal foramen" would be ambiguous and might refer either to the constant foramen in the posterior wall of the ear capsule or to the variable "apertura" in the crista postperilymphatica.

*Platysternon* the apertura vagi is not defined laterally by bone from the fenestra postotica, but is merely a deep notch, while in *Hardella* it is a rather shallow notch. In other testudinoids, however, the opening for the true internal jugular is set off by bone from the fenestra postotica.

The fenestra postotica is usually triangular in form, and we may speak of a "dorsal corner," a ventro-lateral corner," and a "ventro-medial corner." In addition, the columella auris may be seen passing across the fenestra as it extends from the fenestra ovalis to the ear-chamber in the quadrate. Thus, it is sometimes convenient to refer to a "supracolumellar portion of the fenestra postotica" and an "infracolumellar portion of the fenestra postotica." The infracolumellar portion is a rather narrow horizontal slit (for the only structures to pass here are the internal carotid artery and the chorda tympani nerve and Jacobson's and the auricular anastomotic nerves).

Deep within the skull, the supracolumellar portion of the fenestra postotica appears divided into two passageways. The smaller passageway is at the dorsal corner and leads upward and forward between the pro-otic and quadrate bones to open by a foramen into the temporal fossa. This passageway and the foramen forming its opening to the temporal fossa are, respectively, the canalis caroticus externus and foramen carotico-temporale of Siebenrock (1897), while Nick terms the opening "Foramen arteriae facialis," in accordance with a different terminology for the vessel. Actually, the foramen transmits both the temporal stem of the stapedia artery and a branch of the vena capitis lateralis. Since the homology between the stapedia artery and adult human external carotid is far from exact, the differences being in precisely this region, I modify Siebenrock's names to canalis stapediarterialis and foramen stapedio-temporale, *new terms*. While arteria facialis is sometimes used as a name for the stapedia artery of lizards, it has also been used in human anatomy in a different sense; therefore, Nick's name is avoided here.

The larger passageway from the supracolumellar portion of the fenestra postotica leads forward and mesiad to open just lateral to the notch (incisura pro-otica) in the pro-otic bone for the trigeminal ganglion. Nick's (1913) felicitous name for this passageway is canalis cavernosus, while he terms the anterior orifice the foramen cavernosum: since the chief occupant of the passageway and the foramen is that portion of the vena capitis

lateralis homologous with the cavernous sinus of human anatomy, Nick's terminology is here adopted. Essentially, however, the canalis cavernosus of turtles corresponds to the cranioquadrate space or passage of other gnathostomes; the outer wall is formed mainly by the quadrate (with some contribution from the pterygoid, particularly anteriorly), while the bony ear-capsule forms the inner wall. Thus, the facial nerve also runs through the canalis cavernosus from a foramen in the mesial wall of the canalis.

As to the infracolumellar portion of the fenestra postotica, the ventro-mesial corner of the fenestra is set off by a snag of the pterygoid as the foramen caroticum internum of Siebenrock (1897). In the present paper, I use "stapedial artery" for what Siebenrock termed the external carotid, and so "internum" becomes an unnecessary adjective. It seems desirable, however, to make a distinction between a foramen into the pituitary fossa for the carotid, a constant feature of all turtles, and this outermost opening in the skull for the carotid, an opening that shows interesting and taxonomically useful variations. I here propose the name foramen caroticum definitivum for the outermost opening in the skull for the carotid (that is, the internal carotid of many authors); for the foramen into the pituitary fossa (that is, in what ossifies as the basisphenoid) I shall use the name foramen caroticum primitivum (this terminology by analogy to that used for the foramen stylomastoideum in mammals).

The foramen caroticum definitivum leads to a canal that runs forward to the foramen caroticum primitivum. This canal is here called the canalis caroticus. The ventral wall of the canalis caroticus is formed by the pterygoid, the dorsal wall by the ear-capsule; that is, the pro-otic forms the dorsal wall anteriorly, and in *Batagur*, *Callagur*, and *Kachuga trivittata* the opisthotic forms a more posterior continuation of the dorsal wall (and hence, in these genera, the dorsal margin of the foramen caroticum definitivum). In *Morenia* and *Geoclemys* the pterygoid comes to surround the canalis caroticus, and the foramen caroticum definitivum is entirely in the pterygoid. The canalis caroticus gives off two small branches: a posterior branch is given off about opposite the fenestra ovalis to run forward in the pterygoid bone, usually to open onto the dorsal surface of the palate near the anterior extremity of the descending process of the parietal or just anterior to the epipterygoid bone; an anterior, usually minute

branch issues from the canalis caroticus just lateral to the foramen caroticum primitivum or forward of that point and runs forward on the dorsal surface of the pterygoid to disappear or else connect by a diagonal groove with the anterior opening of the canal for the more posterior branch. The more posterior of these canals is the Vidian canal, while the more anterior is here called the canalis arteriopalatinus.

In addition, near the foramen caroticum primitivum there may be a ventral branch of the canalis caroticus that opens onto the pharyngeal surface of the pterygoid. This is here called the canalis carotico-pharyngealis, and its ventral opening, the foramen carotico-pharyngeale. This is a conspicuous foramen in American *Clemmys*, *Terrapene*, *Emys*, and *Emydoidea*, but is small or absent in the other genera.

*Arteries:* The arteries in the head of *Emys orbicularis* and *Testudo (Testudo) graeca* have been described by Shindo (1914) and his findings are summarized in Hafferl (1933). Unfortunately, the few papers on head arteries of turtles have been morphological studies aimed at discovering the basic agreement between all reptiles, and at interpretation of the fate, in the adult, of the aortic arches. While these works have been invaluable in understanding the broad sweep of anatomical specialization and evolution among tetrapods, they are less helpful in understanding the details of phylogeny within one superfamily of testudinoids.

My most satisfactory dissections have been of two beautifully injected *Chrysemys (Trachemys) scripta* prepared by Champlain Biological Supply Company, to whom I bear a great debt of gratitude. Less satisfactory dissections (but adequate at least for the major arteries) have also been made of *Chelydra* (juvenile), *Rhinoclemmys pulcherrima*, *Ocadia*, *Chinemys*, *Testudo*, *Gopherus*, *Chrysemys picta*, and *Malaclemys (Graptemys) geographica*.

After giving off the lingual artery (external carotid of some authors, or ventral carotid) in the anterior part of the neck, the carotid stem continues forward to divide into two branches, a dorsolateral stapedia artery and a ventromedial carotid (or internal carotid). Of the two, the carotid is the smaller.

Almost immediately the stapedia artery gives off small branches to the region of the Eustachian tube, particularly to a structure characteristic of all turtles, but never, to my knowledge,



named or described: the operculum tubae, *new term*. The operculum tubae is a dense, crescentic pad of connective tissue attached by its straight dorsal edge to the posterior extremity of the pterygoid and a roughened area of the quadrate just above the notch for the columella. The convexly rounded ventral border of the operculum tubae hangs down as a free flap held only by loose connective tissue. This flap lies immediately behind the chorda tympani and the Eustachian tube (it is, in all likelihood, a specialization of tissue associated with the posterior wall of the Eustachian tube). The effect of this pad of connective tissue is to press the Eustachian tube closed; however, a branch of the depressor mandibulae muscle (here called the musculus dilator tubae, *new term*) runs from a crest formed by the opisthotic and supratemporal (squamosal of most authors) to the posterior surface of the operculum tubae. Contraction of the muscle draws back the operculum and opens the Eustachian tube. Very likely this is a necessary means of opening the Eustachian tube in a skull with an immovable pterygoid bone, where kinesis of the pterygoid will no longer open and close the adjacent pharyngeal opening of the Eustachian tube. Mammals, faced with a similar problem, have solved it in a different way: by enveloping the Eustachian tube in the swallowing muscles of the velum palatinum, they have made the act of swallowing simultaneously the act of opening the Eustachian tube by muscular massage.

The stapedia artery (arteria temporomaxillaris of Shindo) enters the fenestra postotica in a dorsolateral position, near the dorsal corner of the fenestra. Here, within the skull, between the quadrate and the bony auditory capsule, the artery divides into a dorsal and a ventral branch.

The ventral (mandibular) branch runs with the vena capitis lateralis to exit at the trigeminal aperture. It is usually minute, but large in *Testudo*, *Gopherus*, and *Rhinoclemmys*.

The dorsal (larger) branch passes through the canalis stapediarterialis and out by the foramen stapedio-temporale into the temporal fossa. It is accompanied by a small branch of the vena capitis lateralis. At the foramen stapedio-temporale the artery is divided into a posterior branch running back to the neck along the floor of the temporal fossa (arteria cervicalis of Shindo), and an anterior branch that curves upward and forward and lies in a distinct groove on the external surface of the descending process of the parietal. At about the transverse level of the foramen for



the fifth nerve (but considerably dorsal to the nerve foramen) this anterior branch becomes separated from the parietal and runs through the musculature of the temporal fossa to a point dorso-posterior to the eye; here the artery gives off branches. A small branch (supraorbital) runs above the eye to supply the upper lid and to disappear into a small foramen in the prefrontal, but the main branches (infraorbital) run downward to make contact with the branches of the trigeminal nerve. It is these branches that supply the palate and nasal chamber, essentially following the branches of the nerves. The palate is supplied by a U-shaped artery, continuous across the midline, that runs medial to the border of the triturating surface. This U-shaped artery receives blood mainly from a branch of the suborbital artery that passes through the suborbital foramen or fenestra<sup>1</sup> while a branch of the suborbital artery may join the U shaped artery anteriorly by passing through the nasopalatine foramen. On each side of the mid-line the U-shaped artery gives off a forward branch that enters the nasal chamber from beneath by passing through a pair of foramina (usually near the premaxillo-vomerine suture) that have been called the incisive foramina, but since the incisive foramen of mammalian anatomy is for the duct or ducts of the nasal gland and Jacobson's organ (which are not associated with the foramen of turtles), the foramen cannot be homologous in turtles and mammals. I prefer Seydel's name foramen praepalatium for the foramen of turtles.

The carotid proper (internal carotid) enters the canalis caroticus by the foramen caroticum definitivum, in company with the auricular and Jacobson's nerves.<sup>2</sup> These nerves enter the Vidian canal to join with the palatine ramus of the facial nerve, forming the Vidian nerve; a branch of the carotid, here called the Vidian branch, also enters the Vidian canal to pass forward to the dorsal surface of the palate. The Vidian branch of the carotid is very small. Farther forward, the carotid may give off a small branch that passes through the canalis carotico-pharyngealis to supply the roof of the pharynx. Just lateral to the foramen caroticum primitivum a usually small artery is given off from the carotid to

<sup>1</sup>I term this hole "suborbital foramen" when it is completely filled by the vessels and nerves as in *Malaclemmys*. When the hole in the dried skull is enlarged and mainly filled by membrane in life (e.g. *Clemmys*) I term it the "suborbital fenestra."

<sup>2</sup>I prefer the name "Jacobson's nerve" to "tympanic nerve" for this part of the sympathetic trunk connecting the glossopharyngeal and palatine nerves, since in turtles this nerve is remote from the tympanic cavity.

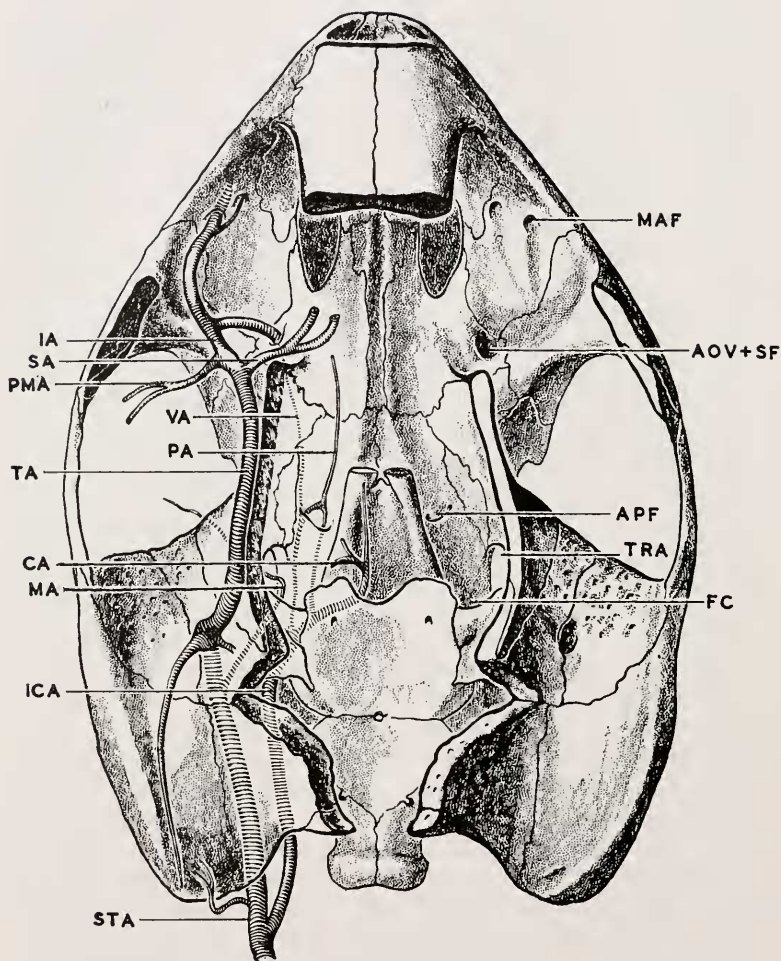


Figure 1. Dorsal view of arterial circulation (left side) and arterial foramina (right side): testudinid pattern (semidiagrammatic), based on *Malaclemys (Graptemys) geographica*. Abbreviations: AOV+SF, anterior orifice of Vidian canal and suborbital foramen; APF, foramen arterio-palatinum; CA, cerebral carotid artery; FC, foramen cavernosum; IA, infraorbital artery; ICA, (internal) carotid artery; MA, mandibular artery; MAF, maxillary arterial (alveolar?) foramen; PA, palatine artery; PMA, pseudomandibular branch of infraorbital artery; SA, supraorbital artery; STA, stapedial artery; TA, temporal portion of stapedial artery; TRA, trigeminal aperture; VA, Vidian artery.

run forward in the canalis arteriopalatinus of the pterygoid (usually a tiny groove, rather than a closed canal). To judge from the size of the bony foramen, this is a moderately large artery in *Batagur*, *Callagur*, *Kachuga*, *Morenia*, *Hardella*, *Orlitia* and *Siebenrockiella*. This artery has the position of the artery indicated by grooves on the parasphenoid of labyrinthodonts and there called the palatine artery,<sup>1</sup> and accordingly, I term it the palatine artery here, although in most Testudinidae it appears to be a vestigial, almost functionless structure. The artery of much larger size seen in sea turtles and called the arteria palatino-nasalis by Nick (1913) appears to be homologous in that it is a forwardly directed branch of the carotid that is separated from the cerebral carotid by the trabecula cranii (represented in the adult by the lateral border of the pituitary fossa of the basisphenoid). There is usually an anastomotic artery between the Vidian and palatine arteries.

The carotid enters the foramen caroticum primitivum to pass into the pituitary fossa. Here there is a small anastomosis between the left and right arteries behind the pituitary (presumably, a circle of Willis), but the main artery (now the arteria carotis cerebialis) breaks up into branches in the meninges.

To generalize, apart from vestigial twigs, the separation between carotid and stapediaal arteries in Testudinidae and *Chelydra* represents a segregation of blood for the brain (carotid) from blood for the rest of the head (stapediaal artery). Furthermore, the stem of the supraorbital and infraorbital arteries is extracranial.

## II. THE PATTERN OF THE KINOSTERNIDAE

*Bony canals and foramina*:—I have been able to examine skulls of *Kinosternon*, *Sternotherus*, *Claudius*, *Staurotypus*, and *Dermatemys*. The most conspicuous difference from the testudinid condition is the absence of the canalis stapediaarterialis and foramen stapedio-temporale, or else the reduction of the canal to a very small pore. The foramen caroticum definitivum is relatively larger than that of testudinids, as is the canalis caroticus. The canalis caroticus leads forward to the level of the pituitary fossa and there divides into two openings: the outer and larger opening

<sup>1</sup> For a brief review of the position of the groove for the palatine (= palatal = nasopalatine) artery in labyrinthodonts see Romer (1947, pp. 44-45, fig. 8).

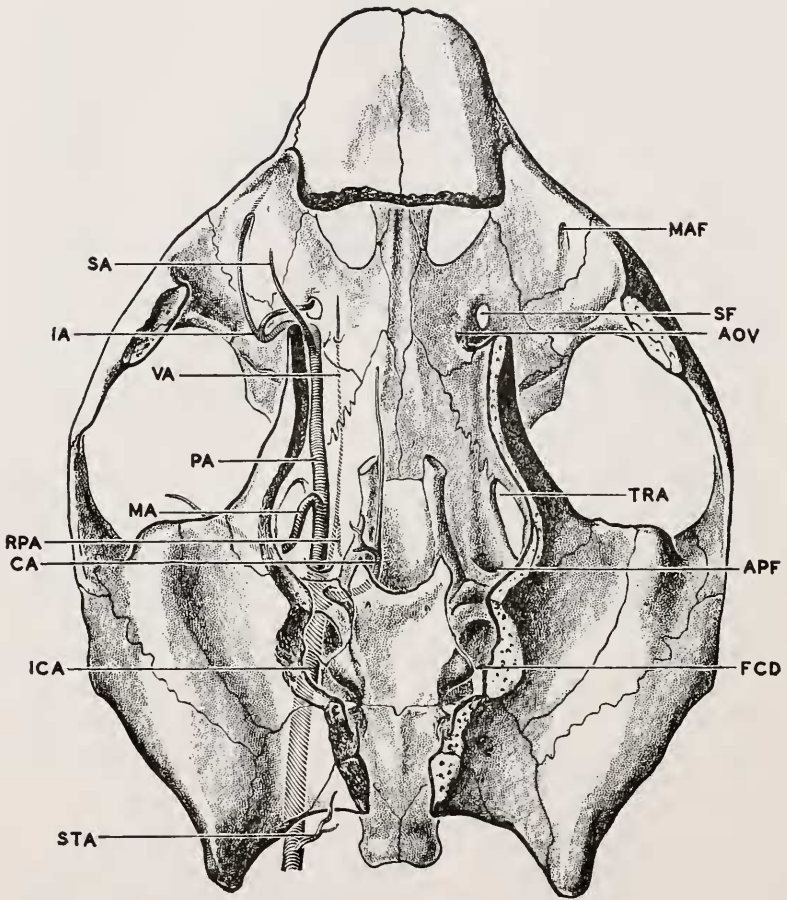


Figure 2. Dorsal view of arterial circulation (left side) and arterial foramina (right side): kinosternid pattern (semidiagrammatic), based on *Kinosternon sonoriense*. Abbreviations as in Figure 1; also, AOV, anterior opening of Vidian canal; FCD, foramen caroticum definitivum; RPA, recurrent pharyngeal branch of Vidian artery (a small artery supplying pharyngeal epithelium and passing through the pterygoid by the foramen carotico-pharyngeale); SF, suborbital foramen.

is that of the canalis arteriopalatinus, while the smaller, inner opening is the foramen caroticum primitivum. The opening of the canalis arteriopalatinus is ventral to the foramen cavernosum and is separated from that foramen by an horizontal lamina of the pterygoid. For convenience we may call this anterior opening of the canal the foramen arteriopalatinum, *new term*.

The Vidian canal is small and runs forward from an opening in the floor of the canalis arteriopalatinus. The Vidian canal is entirely buried in the pterygoid bone.

*Arteries.* I have dissected an injected *Sternotherus odoratus*, two uninjected *Kinosternon subrubrum*, and one uninjected *Kinosternon sonoriense*. The stapedial artery appears to be all but absent; in the *Sternotherus* and *K. sonoriense* a minute artery extended dorsally from the carotid stem behind the head and supplied the muscles at the rear of the temporal fossa; this probably represented the stapedial. In the *Kinosternon* specimens, branches of the vena capitis lateralis passed from the temporal fossa into a very small vestige of the foramen stapedio-temporale. Probably the occasional vestiges of this foramen seen in other Kinosternidae are similarly purely venous.

The carotid divides into a smaller arteria carotis cerebialis passing through the foramen caroticum primitivum and similar to that of testudinids, and a larger arteria palatina passing through the foramen arteriopalatinum. The blood for head structures other than the brain comes from the palatine artery. The palatine artery gives off a main (mandibular) branch that accompanies the mandibular nerve and supplies the jaw muscles, then, still within the cavum epiptericum, the palatine artery continues forward as a large vessel to the orbital region, where it breaks up into supraorbital and infraorbital branches distributed as in Testudinidae.

To generalize, in Kinosternidae nearly all the blood of the head passes through the canalis caroticus, and it is not until the single main head artery reaches the trabecula cranii and foramen caroticum primitivum that there is a segregation of blood for the brain from blood for the remainder of the head. This segregation takes place not behind the skull, as in Testudinidae, but within the cavum epiptericum. Further, the stem of the infraorbital and supraorbital arteries is intracranial.



## III. DISCUSSION

In terms of the bony canals for arteries, the Testudinoidea (sense of Romer 1956) fall into two groups. One group contains *Chelydra*, *Macrolemys*, and the Testudinidae of Romer (1956). The other group contains *Dermatemys*, the Staurotypinae, and the Kinosterninae of Romer (1956). In testudinids there is a large foramen stapedio-temporale, but the foramen arteriopalatinum is small or minute. In the kinosternines the foramen stapedio-temporale is minute or absent, while the foramen arteriopalatinum is very large and conspicuous.

It would seem, since blood for the head other than the brain must come through one or the other of these foramina (except in land tortoises and some geoemydides,<sup>1</sup> where the mandibular branch of the stapedia is large), that reduction of the one foramen must lead to increase in the other. However, it does not seem likely that the testudinid condition is derived from the kinosternine pattern, for a large foramen stapedio-temporale, and, by inference, a well-developed temporal branch of the stapedia artery, is found in all turtles except the *Dermatemys*-Kinosterninae-Staurotypinae series, even in the Amphichelydia; moreover, this, the testudinid, type of stapedia artery is the type seen in Squamata, Rhynchocephalia, and Crocodylia.

On the other hand, the reduction of the palatine artery and consequent reduction of the foramen arteriopalatinum seen in Testudinidae and Chelydrinae is also a departure from the condition in other turtles and indicates a specialization in the opposite direction from that of kinosternines. Even in *Morenia*, *Orlitia*, and *Batagur*, where the foramen arteriopalatinum is the largest to occur in testudinids, the foramen is decidedly smaller than the foramen caroticum primitivum. Both arterial types might be derived from a pattern such as that of sea turtles (see Nick 1913 and Shindo 1914), where there is both a strong stapedia artery, primarily supplying the jaw musculature, and a strong palatine artery, primarily supplying the nasal and palatal region. The kinosternine pattern may be derived from this, probably primitive, pattern, by capture of the temporal circulation by the palatine artery, while the testudinid pattern may be derived by capture of the nasal and palatal circulation by the stapedia artery.

<sup>1</sup>I use the ending "-ide" for a suprageneric taxon to which I cannot yet assign with confidence a place in the taxonomic hierarchy.

Within each of the two groups of Testudinoidea, as defined by head arterial foramen pattern, there is relatively little variation. The most notable is that seen in *Gopherus* and some species of *Geochelone* (e.g., *G. pardalis* and *G. denticulata*, but not *G. gigantea* and *G. radiata*). Here, the lower (mandibular) ramus of the stapedia artery does not accompany the vena capitis lateralis anteriorly, but makes exit to the temporal fossa through its own foramen, here called foramen arteriomandibularis, *new term*, lying lateral to the foramen cavernosum. Other than this, the land tortoises are very similar to pond turtles, and their classification together in one family, Testudinidae, seems thoroughly warranted. (A foramen arteriomandibularis occurs as a variation in *Rhinochelymys* and is always potential where the ramus mandibularis is large.)

The present findings do not, however, support the classification of Williams (1950) or its expanded form given in Romer (1956) in all details. This classification placed *Dermatemys* in a separate family (along with certain poorly known fossil genera), the Dermatemydidae; *Chelydra* and *Macrochelys* (syn. *Macrochelys*) formed the Chelydrinae, *Claudius* and *Staurotypus* the Staurotypinae, and *Kinosternon* and *Sternotherus* the Kinosterninae of a family Chelydridae;<sup>1</sup> *Platysternon* formed the Platysterninae, the pond turtles the Emydinae, and the land tortoises the Testudininae of a family Testudinidae. While the foramina for arteries in the main conform to this classification, particularly on such points as the close relationship between *Platysternon*, the pond turtles, and the land tortoises, and the close relationship between the Kinosterninae and the Staurotypinae, the arterial foramina suggest that *Dermatemys* is much more closely related to the Staurotypinae than is indicated by Williams' classification, and that *Chelydra* and *Macrochelys* are more closely related to the Testudinidae than to the remainder of Williams' Chelydridae. As here interpreted, *Chelydra* and *Macrochelys* are already committed to the testudinid evolutionary line in the reduction of the palatal artery (much more reduced than in many Old World emydines), while *Dermatemys* is committed to the kinosternid evolutionary line in its loss of the stapedia artery as indicated by the absence of a foramen stapedio-temporale.

*Dermatemys*, *Staurotypus*, and *Claudius* were grouped together by Boulenger (1889) in the Dermatemydidae. While later

<sup>1</sup>This association of kinosternines, staurotypines, and chelydrines in one family appears to date from Gray 1870.



work has demonstrated Boulenger's error in separating *Staurotypus* and *Claudius* from the kinosternines, the affinity between *Dermatemys* and the Staurotypinae suggested by Boulenger seems much more real to me than does the suggested affinity of the staurotypines and kinosternines with *Chelydra* and *Macrolemys*.

Several other points suggest that kinosternines are close to *Dermatemys*, while *Chelydra* and *Macrolemys* are close to the Testudinidae. Thus the kinosternines and *Dermatemys* have a conical and radially symmetrical footplate of the columella auris, while the footplate in chelydrines is flattened and disc-like, with the shaft arising from below the center; most testudinids have a columella as in chelydrines, but some Asiatic forms (e.g. *Moronia*, *Batagur*, *Orlitia*) approach kinosternines in the conical form of the footplate, although the asymmetry is marked.

Again, in kinosternines and *Dermatemys* there is a tight suture between basioccipital and opisthotic behind the acoustic papilla of the inner ear; *Chelydra* and *Macrolemys* agree with Testudinidae in the presence of an open fissure in the suture behind the apex of the papilla. Further, cloacal bursae are absent in *Dermatemys* and kinosternines, but present in *Chelydra* and *Macrolemys*; most aquatic Testudinidae have bursae (Smith and James).

The genus *Baptemys*, of the North American Eocene, appears to be intermediate morphologically between *Dermatemys* and the kinosternines. The genus is known from a number of shells, a few fragments of the limb skeleton, and two partial skulls. Of the skulls, one (in the Yale University Peabody Museum) is nearly complete. I have examined this skull and find it quite as figured by Hay (1908, pl. 37).

*Baptemys* agrees with both *Dermatemys* and the kinosternines in the absence of the foramen stapedio-temporale, the great forward extent of the posterior temporal emargination, and the entrance of the squamosal (quadrato-jugal Auct.) into the border of the posterior temporal emargination so that the postorbital is broadly excluded from the supratemporal (squamosal Auct.). *Baptemys* agrees with *Dermatemys* and differs from the kinosternines in: 1) having a moderately deep inferior temporal emargination; 2) having the trochlear process of the crista prae-temporalis concealed from lateral view by the temporal arch; 3) having rather large frontals, with the interfrontal suture longer than the interprefrontal suture. *Baptemys* agrees with

kinosternines and differs from *Dermatemys* in: 1) absence of keels on the triturating surfaces; 2) high, acute coronoid process of the lower jaw; 3) lack of serrations on the jaw margins; and 4) reduction of the plastron. In one feature, *Baptemys* differs from both *Dermatemys* and the kinosternines: there is a complete series of neurals, separating the pleurals on the midline throughout the carapace.

It should be noted that the genera among the testudinid group that come nearest to the *Dermatemys*-kinosternine series are not *Chelydra* and *Macrochelys*, but the Asiatic *Batagur-Morenia*-series, where the foramen arteriopalatium is less reduced than in other Testudinidae and the footplate of the columella auris is conical. The general appearance of the skull of *Dermatemys* is strongly reminiscent of *Batagur* and *Hardella*, particularly in such features as upturned nares, broad and complexly ridged triturating surfaces and broad muscular tuberosities of the basioccipital. This resemblance extends to the pes, for *Dermatemys* agrees with *Hardella*, *Kachuga*, *Callagur*, and *Batagur* in having four phalanges in the fifth toe (usually there are three or two phalanges in this toe in Testudinoidea).

Thus Asiatic "batagurs," on the one hand, and the Central American *Dermatemys*, on the other, appear to be near the base of the divergence of the testudinid and kinosternid series.

#### ACKNOWLEDGEMENTS

For the loan of material, I am grateful to Dr. Doris Cochran (United States National Museum), Dr. Norman Hartweg (University of Michigan Museum of Zoology), and Dr. Ernest Williams (Museum of Comparative Zoology). The Champlain Biological Supply Company most generously provided dissection material of *Chrysemys (Trachemys) scripta*. For aid, both athletic and moral, in the examination of the Yale Peabody Museum skull of *Baptemys*, I am in debt to Mr. Peter Robinson. I have profited much from discussions of turtle morphology with Dr. Williams and with Dr. Thomas Parsons. Without the aid of my wife, Rosa McDowell, in the preparation of the manuscript, this paper would have been impossible.

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